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Invited Commentaries

Describing mate choice in a biased world: comments on Edward and Dougherty & Shuker

Hanna Kokko^a and Michael D. Jennions^b

^aInstitute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland and ^bEvolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra, Australian Capital Territory 0200, Australia

Edward (2015) asks the reader if we are correctly modeling and measuring choosiness and preference functions—response curves that give the probability (y axis) that a focal individual will mate with a potential mate with a given phenotype (x axis). We agree that thinking about potential pitfalls is worthwhile. We would, however, like to offer some counterpoints that reflect our view that his concerns, while often technically correct, lead to headaches that abate if one swallows a dose of biological pragmatism.

First, Edward (2015) notes that choosy individuals need not have a lower mating rate than nonchoosy ones: nonchoosers might be generally less responsive so that their preference functions are not only flat but also vertically displaced downward relative to that of choosy individuals. This is possible, but when formulating a *null hypothesis*, it is a strange to assume that responsiveness covaries with the shape of preference functions. We consider it more biologically meaningful to remember that active mate choice typically involves rejecting some prospective mates. This lowers the mating rate relative to that were the *same individual* to mate indiscriminately (e.g., Johnstone et al. 1996). Indirect mate choice (Wiley and Poston 1996), not mentioned by Edward, offers the best counter examples to the above rule: consider “hilltopping” where females indirectly choose males by going to a specific location to mate. By travelling to a hilltop they might minimize their own time to mating. Even so, the fact that mate choice *usually* lowers the mating rate remains true—especially for species used in standard two-choice mating experiments (i.e., species where mate rejection occurs).

Second, many of Edward’s technical arguments rely on the complete absence of mate assessment by nonchoosy individuals. This is ultimately untenable. The need to distinguish between inanimate and animate objects, between predators and conspecifics, and so on, mean that all animals that mate engage in mate assessment (i.e., have a minimum threshold). Otherwise they would spontaneously mate “at random” with the world. This is not to say that mistakes are not made—witness male beetles in Western Australia attempting to copulate with discarded beer bottles (Gwynne and Rentz 1983). One can fret about the appropriateness of equating a very low mating threshold with being nonchoosy, but excessive worrying is cured by pragmatically defining a frame of reference. If every (or almost every) member of the opposite sex is above an individual’s

mating threshold, it is sensible to describe him/her as being nonchoosy. The abstraction of potential mates that do not, but could in principle, exist is unhelpful.

Individuals can mate rarely despite being nonchoosy, but the opposite is unlikely: it is difficult to be very choosy and still mate as often as a promiscuous nonchoosy individual (Kokko and Mappes 2013). This important asymmetry makes the nonguaranteed nature of mating rate reductions experienced by choosy individuals less troublesome in practice than in Edward’s account. We confess to fondness for the notion that costs of choosiness usually manifest as a lower mating rate because many theoreticians, ourselves included, make predictions based on it. This is why, for example, theory predicts that (a) females are usually choosier than males (here mate availability differences mainly arise from sex differences in parental investment) (e.g., Johnstone et al. 1996) and (b) two-choice mating experiments can reveal choosiness that might be completely, and adaptively, absent in no-choice tests (Barry and Kokko 2010). This brings us to Dougherty and Shuker (2015), who investigated support for (a) and (b) with a meta-analysis of experimental mate choice studies. Only the latter prediction was supported. Why?

We can think of a few reasons, but we focus on a key one: the analysis did not involve paired comparisons. Studies of males involve a different set of species than those of females. It seems likely that researchers conduct male choice studies on species where there is at least circumstantial evidence that males are choosy. This will inflate the estimated mean strength of male mate choice compared with that from a truly random sample of species. Similar selective testing is likely to occur for studies of female choice, but the bias is magnified for males if, as theory predicts, the true proportion of species where mate choice is weak or absent is higher for males than females. Extrapolating from a meta-analysis to the broader context requires care if there is a strong research bias (Jennions et al. 2013). In a thought experiment, we might ask “Do mammals fly?” The more nonwinged species in our sample, the smaller the effect size until the answer is statistically “no.” In this thought experiment, it is easy to identify the problem: the presence or absence of wings should have been included as an important modifier variable. Unfortunately, the source of real-world variation among species for biologically intriguing questions is usually far less clear.

The theoretical prediction (b) was confirmed. Is the matter settled for this one question at least? We believe that intriguing issues still remain. Biases might confound the comparison between choice and no-choice experimental designs as these designs often use different criteria for choice (e.g., association time vs. latency to mate). Also, with a choice design, if neither potential mate was chosen, then a trial is discarded as the test subject was sexually unresponsive rather than classified as rejection of both mates. In contrast, in a no-choice design, the failure to mate (or a pitiful performance for the behavioral proxy of mating) is often treated as mate rejection. Consequently, no-choice designs are systematically biased toward including data

from nonsexually responsive individuals, which underestimates the strength of sexual selection. It is therefore worth confirming that the difference between the 2 study designs persists if the meta-analysis is confined to no-choice studies that ensured test subjects were sexually receptive.

Finally, a no-choice design is a good proxy for a natural situation in which prospective mates are encountered sequentially, but two-choice designs are often a major simplification for species that often encounter numerous prospective mates simultaneously (e.g., fiddler crabs, chorusing frogs and insects, lekking birds, and mammals). Given that experimental data suggest that the number of mates can affect mate choice decisions (Hutchinson 2005), we are unlikely to run out of intriguing study questions any time soon.

Address correspondence to H. Kokko. E-mail: hanna.kokko@ieu.uzh.ch.

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The multiple components of mate choice: a comment on Edward and Dougherty & Shuker

Courtney L. Fitzpatrick^a and Maria R. Servedio^b

^aNational Evolutionary Synthesis Center (NESCent), 2024 W. Main St. Suite A200, Durham, NC 27705-4667, USA and ^bDepartment of Biology, University of North Carolina, CB# 3280, Coker Hall, Chapel Hill, NC 27599, USA

To the uninitiated, “mate choice” may sound like a simple concept, but 2 articles in the current issue of *Behavioral Ecology* show that it is, in fact, quite multidimensional. Although the pair of articles by Edward (2015) and Dougherty and Shuker (2015) bring us greater understanding of many points, they also reveal much that still remains obscured.

Edward (2015) points out that behavioral ecologists use inconsistent language to describe key components of mate choice. Although he does not attempt the Sisyphean task of standardizing the diverse

vocabulary in the previous literature (although he does begin this endeavor in an illustrative table), he makes great strides in starting what we hope will be a dialogue about the ideal usage of terms describing mate choice. Two components of mate choice whose properties merit further exploration, for example, are mating rate and acceptance thresholds. Edward makes the important point that mating rate should be constrained by the presence of potential mates; in particular, he argues that when a species uses an acceptance threshold, mating rate will change as the threshold shifts (e.g., Edward's Fig. 1j). If all else is equal, however, it seems that a shift in *any* preference function (i.e., not just a threshold function) that reduces overlap with the distribution of available mates should also lead to a change in mating rate (e.g., including when there is a normally distributed function such as in Edward's Fig. 1m). Additionally, several unique properties attributed to acceptance thresholds seem to be consequences of the fact that the threshold marks a change (whether as a step function or as a sigmoid) from absolute rejection to absolute acceptance. But why cannot thresholds instead demark a change between a low and high *probability* of acceptance, rather than just 0 or 1? If this were the case, we can imagine that mating rate may be under independent control and fixed; a shift in the threshold (i.e. horizontal in Edward's Fig. 1) could then be compensated by a corresponding change in the relative probabilities of acceptance on either side of the threshold (i.e. vertical in Edward's Fig. 1).

While stressing the importance of vocabulary, Edward implicitly cautions theorists not to sweep consideration of the many components of mate choice under the rug. Although we agree that theoreticians must be very careful in their assumptions, we counter that many of these details may not, in fact, make a difference to a model's conclusions. If there is a good reason to believe this is the case, it would be a mistake to dismiss models that do not make unnecessarily complicating assumptions. The purpose of models is to isolate the effects of certain factors by placing them in as simplified a context as possible.

The central point made by Dougherty and Shuker (2015) is also an important one; the type of choice trial that researchers use can influence the strength of their measured effects. We applaud their careful meta-analytic methodology and their tests for phylogenetic effects and publication bias. They find that the effect size for preference was significantly stronger when choice tests were used instead of a no-choice paradigm. The 2 plausible explanations that they provide (cognitive constraints and opportunity costs) dovetail with one of the most important take-aways from this article; those of us interested in mate choice studies must consider the natural history of the organism in order to design the appropriate choice test.

Using a meta-analytic conversion, Dougherty and Shuker compare the strengths of preference not only between choice and no-choice tests but also between preferences in males and females and between choices that are intrapopulation, interpopulation, and interspecies (within choice and no-choice tests). They obtain the puzzling findings that there are no statistical differences in these latter two comparisons. These results are clear departures from the expectations that female choice should be stronger than male choice (because, on average, females are the choosier sex) and that preferences across versus within a species should differ more than preferences solely within a species. Although the authors caution readers against overinterpretation based partly on small sample sizes, the results nonetheless require explanation and potentially suggest biases that may have been overlooked. The discussion closes with proscriptions that we support; experimental research on mate choice should assess the strength of preference under *both* choice and no choice paradigms, whenever possible, using the same subjects for both to control for individual effects.